# Tip dating supports novel resolutions of controversial relationships among early mammals

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THE ROYAL SOCIETY B
BIOLOGICAL SCIENCES

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|---|---|
| Journal: | *Proceedings B* |
| Manuscript ID | RSPB-2020-0943.R1 |
| Article Type: | Research |
| Date Submitted by the Author: | n/a |
| Complete List of Authors: | King, Benedict; Naturalis Biodiversity Center; Flinders University<br>Beck, Robin; University of Salford, Manchester, School of Environmental and Life Sciences |
| Subject: | Evolution < BIOLOGY, Palaeontology < BIOLOGY |
| Keywords: | tip-dating, Bayesian, Haramiyida, Allotheria, Juramaia |
| Proceedings B category: | Palaeobiology |
| | |

## Author-supplied statements

Relevant information will appear here if provided.

### *Ethics*

*Does your article include research that required ethical approval or permits?:*
This article does not present research with ethical considerations

*Statement (if applicable):*
CUST_IF_YES_ETHICS :No data available.

### *Data*

*It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:*
Yes

*Statement (if applicable):*
Full data, analysis code, files and results are on figshare (https://doi.org/10.6084/m9.figshare.8040158).

### *Conflict of interest*

I/We declare we have no competing interests

*Statement (if applicable):*
CUST_STATE_CONFLICT :No data available.

### *Authors' contributions*

This paper has multiple authors and our individual contributions were as below

*Statement (if applicable):*
BK and RB designed the study. BK performed analyses and produced figures. BK and RB wrote the paper.

# Tip dating supports novel resolutions of controversial relationships among early mammals

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## Abstract

The estimation of the timing of major divergences in early mammal evolution is challenging due to conflicting interpretations of key fossil taxa. One contentious group is Haramiyida, the earliest members of which are from the Late Triassic. Many phylogenetic analyses have placed haramiyidans in a clade with multituberculates within crown Mammalia, thus extending the minimum divergence date for the crown group deep into the Triassic. A second taxon of interest is the eutherian *Juramaia* from the Middle-Late Jurassic Yanliao Biota, which is morphologically very similar to eutherians from the Early Cretaceous Jehol Biota and implies a very early origin for therian mammals. Here we apply Bayesian tip-dating phylogenetic methods to investigate these issues. Tip dating firmly rejects a monophyletic Allotheria (multituberculates and haramiyidans), which are split into three separate clades, a result not found in any previous analysis. Most notably, the Late Triassic *Haramiyavia* and *Thomasia* are separate from the Middle Jurassic euharamiyidans. We also test whether the Middle–Late Jurassic age of *Juramaia* is 'expected' given its known morphology by assigning an age prior without hard bounds. Strikingly, this analysis supports an Early Cretaceous age for *Juramaia*, but similar analyses on twelve other mammaliaforms from the Yanliao biota return the correct, Jurassic age. Our results show that analyses incorporating stratigraphic data can produce results very different from other methods. Early mammal evolution may have involved multiple instances of convergent morphological evolution (e.g., in the dentition), and tip dating may be a method uniquely suitable to recognising this due to the incorporation of stratigraphic data. Our results also confirm that *Juramaia* is anomalous in exhibiting a much more derived morphology than expected given its age, which in turn implies very high rates of evolution at the base of therian mammals.

Key words: tip dating, Bayesian, Haramiyida, Allotheria, Juramaia, Mammals, Mammaliaforms

# Introduction

Allotherians are an extinct group of mammaliaforms, primarily known from the Mesozoic, that are currently the subject of conflicting phylogenetic hypotheses (figure 1). Allotherians share a number of dental apomorphies, most notably postcanines with multiple cusps in longitudinal rows (superficially resembling those of some therian mammals, such as rodents), and they include haramiyidans, multituberculates and gondwanatherians [1-6]. Some phylogenetic analyses have supported monophyly of Allotheria, within (crown-clade) Mammalia [2, 7-10](figure 1, topology 1). Conversely, others have recovered haramiyidans outside Mammalia, but with multituberculates remaining within Mammalia [3, 11, 12](figure 1, topology 2a), suggesting that allotherian dental apomorphies have evolved more than once. Finally, two studies recovered diphyletic haramiyidans, with the euharamiyidans forming a clade with multituberculates within crown mammals, but the Triassic species *Haramiyavia* and *Thomasia* falling outside the crown group [13, 14] (figure 1, topology 2b).

Monophyly versus polyphyly of Allotheria has major implications for our understanding of Mesozoic mammal evolution, leading to different scenarios for the evolution of numerous dental and skeletal features, including the so-called 'Definitive Mammalian Middle Ear', in which the angular, articular, prearticular, and quadrate have become entirely auditory in function, and are fully separated from the jaw joint [9, 15, 16]. It also affects interpretations of the age of Mammalia: if Late Triassic haramiyidans such as *Haramiyavia* and *Thomasia* fall within the crown-clade, then the split between monotremes and therians must be at least this old [8]; if they fall outside the crown-clade, this split could be considerably younger, as it would render *Asfaltomylos* and *Henosferus* (which appear to be early relatives of monotremes) from the Middle Jurassic of Patagonia the oldest known members of the crown-clade [17].

Another fossil mammal that has been the subject of recent discussion is the eutherian *Juramaia sinensis* from the Middle–Late Jurassic (164–159 million year old) Linglongta Biota (the younger of the two phases composing the Yanliao/Daohugou Biota) from the Lanqi/Tiaojishan Formation of China [18, 19]. Based on its known morphology, *Juramaia* has been argued by some authors [20-22] to be 'unexpectedly advanced' for its age, as it closely resembles eutherians from the much younger (ca. 126 Ma) Jehol Biota[20, 22]. By contrast, the same has not been argued for other mammaliaforms from the Yanliao Biota. However, whether or not the known morphology of *Juramaia* is 'unexpected' given its age has never been quantitatively tested.

Tip-dated phylogenetic methods [23], which include morphological and stratigraphic data in a single analytical framework, are a promising avenue to investigate these issues. The wide time difference between the earliest known haramiyidans (Late Triassic) and the oldest known multituberculates (Middle Jurassic)[5, 24] suggests that their similarities may be the result of convergent evolution, and incorporating stratigraphic data into phylogenetic analysis means that this temporal disparity is taken into account [25]. Another use of tip dating is to use the morphological data to inform the ages of fossils with uncertain dates [26, 27]. Given that the known morphology of *Juramaia* has been identified as 'unexpectedly advanced' [20-22], it can be used to test whether tip dating continues to support a Middle–Late Jurassic age when its age is allowed to vary. Here we apply tip dating to recent datasets of Mesozoic mammals to investigate the relationships of the haramiyidans, and to test the congruence between the known morphology and age of *Juramaia* and other Yanliao mammaliaforms.

# Materials and Methods

Our focal dataset was taken from Huttenlocker *et al.* [3], which comprises 538 morphological characters scored for 125 mammaliaforms and non-mammaliaform cynodonts. Because the sampling of Cenozoic taxa in this dataset was extremely sparse relative to Mesozoic taxa, extant and Cenozoic fossil taxa were pruned from the dataset, and invariant characters in this reduced dataset were deleted, leaving 96 taxa and 507 characters. Tip-dated Bayesian analyses were performed in BEAST v2.5.2 [28]. The Markov model for variable characters (hereafter Mkv) was used [29], with a gamma distribution (with four rate categories) to account for rate variation across sites. Characters were partitioned according to the number of character states. The clock model was an uncorrelated lognormal clock [30], and the tree prior was a sampled-ancestor fossilised birth-death model [31]. Tip dates were assigned uniform priors across the range of uncertainty for each taxon. The analysis was run for 1 billion generations, sampling every 500,000. Convergence of four independent runs was confirmed in Tracer [32], and the R package RWTY [33]. To investigate conflicts between the different parts of the dataset of Huttenlocker *et al.* [3], and further test allotherian relationships, the following character subsets were analysed individually: craniodental, dental only, and postcranial only. Undated Bayesian analyses were performed in MrBayes [34], again using the Mkv model with a gamma distribution (with four rate categories) to account for rate variation across sites. Four independent runs, each with four chains, were run for 10 million generations, sampling every 5000. Parsimony analyses in TNT [35] employed new technology search, using sectorial search and tree fusing with default settings for 1000 random addition sequences, followed by TBR swapping to fully

explore tree islands. We also ran a constrained parsimony analysis with a negative constraint on haramiyidan monophyly.

To further test the extent to which tip dating could overturn topologies supported under other methods, similar tip-dated analyses were run on the datasets of Krause *et al.* [2] and Wang *et al.* [15], both of which originally recovered a monophyletic Allotheria. Extant taxa were pruned, as above, resulting in datasets of 81 taxa, 448 characters and 89 taxa, 473 characters respectively. Tip-dated analysis of the Krause *et al.* dataset showed very poor mixing (caused by alternative likelihood peaks representing monophyly or polyphyly of Allotheria) and was therefore run for 32 independent runs, each of a billion generations to obtain reliable estimates of the relative posterior probabilities of the two phylogenetic hypotheses. Results from each run were thinned (sampling every 5 million generations) and, following removal of a 50% burn-in from each run, combined for further analysis.

We also ran an analysis of the Huttenlocker *et al.* [3] dataset with a wider prior age range for *Juramaia*. This represents a quantitative test of the ability of tip dating to infer the age of *Juramaia* based on its known morphology. The tip-age prior for *Juramaia* was modified to a Laplace distribution centred on 161 MYA, with a scale parameter of 8. This represents a strong prior expectation that *Juramaia* is Jurassic in age (with 90% of the prior probability density between 143 and 179 MYA), but due to the absence of hard maximum or minimum bounds, dates outside this range are permitted. The other taxa from the Yanliao Biota in this dataset (*Agilodocodon, Arboroharamiya, Castorocauda, Docofossor, Maiopatagium, Megaconus, Pseudotribos, Rugosodon, Shenshou, Vilevolodon, Xianshou linglong* and *Xianshou songae*), were given the same Laplace distribution prior in separate analyses, to test the effectiveness of this method. Extraction of branch rates from the consensus trees for plotting (figure S13) used the R package OutbreakTools [36].

# Results

*Allotherian relationships*

Tip-dated analysis of our focal dataset, modified from Huttenlocker *et al.* [3], resulted in allotherian taxa falling into three separate clades (figure 2). The Late Triassic haramiyidans *Haramiyavia* and *Thomasia* are placed outside Mammaliaformes, in a strongly-supported clade with tritylodontids (posterior probability (PP) = 0.91). The Middle Jurassic euharamiyidans, Early Cretaceous hahnodontids, and the Late Cretaceous Madagascan gondwanatherian *Vintana*, by contrast, collectively form a strongly-supported clade (PP =1.00) within Mammaliaformes, although our phylogeny is insufficiently well resolved to indicate whether or not this is within crown-clade

Mammalia. Finally, the multituberculates form a third strongly supported clade (PP = 1.00), within Mammalia.

Both undated Bayesian and parsimony analysis recovered monophyletic Haramiyida (table 1). Parsimony analysis with a negative constraint on haramiyidan monophyly (i.e. preventing *Haramiyavia* and *Thomasia* from forming a clade with euharamiyidans) produce trees that are only two steps longer (representing just a 0.1% increase in tree length) than the unconstrained trees. Constrained and unconstrained trees were not significantly different (p=0.87) under the Templeton test [37].

Support for monophyly of Allotheria and of Haramyida is driven by dental characters, and it should be noted that *Thomasia* is known only from isolated teeth and that *Haramiyavia* is also represented almost exclusively by dental characters. Analysis of craniodental or dental only character subsets led to allotherians falling into progressively fewer separate clades across tip-dated, undated and parsimony methods (table 1; figures S3–5). Strong support for allotherian polyphyly (i.e. three independent clades) is only found under tip dating on the full dataset, whereas all methods support allotherian monophyly when dental characters are considered in isolation. Tip-dated analysis of postcranial characters only also recovers separate euharamyidan and multituberculate clades (figure S5), but *Haramiyavia*, *Thomasia*, hahnodontids and *Vintana* could not be included in this analysis as postcranial remains have not been described for them [13, 38].

| **Method** | **Tip-dated Bayesian** | | | | **Undated Bayesian** | | | | **Parsimony** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Topology** | **1** | **2a** | **2b** | **3** | **1** | **2a** | **2b** | **3** | **1** | **2a** | **2b** | **3** |
| **Complete dataset** | 0.0 | 5.7 | 0.0 | 94.3 | 0.0 | 71.9 | 0.0 | 28.0 | | | | |
| **Craniodental** | 0.2 | 59.5 | 12.9 | 27.4 | 0.3 | 1.7 | 92.8 | 5.0 | | | | |
| **Dental** | 96.8 | 0.0 | 0.0 | 0.0 | 98.9 | 0.0 | 0.0 | 0.0 | | | | |

**Table 1. Support for different configurations of the "Allotheria" across phylogenetic reconstruction methods and data subsets**. Topologies refer to the number of independent clades formed by the three allotherian groups (see figure 1): Numbers are posterior probabilities in percentage form. Shaded cells refer to the topology found in the consensus tree (50% majority rule for Bayesian and strict consensus for parsimony).

Tip dating using the Wang *et al.* [15] dataset recovered a diphyletic Haramiyida (figure S6), with euharamiyids and multituberculates forming a clade distant from *Haramiyavia* + *Thomasia* (figure 1, topology 2b). The dataset of Krause *et al.* [2] led to a more complex result, as the sample of post-burn-in trees includes some topologies in which Allotheria is polyphyletic and others in which it is monophyletic. This analysis showed 'twin peak' behaviour of the prior and likelihood traces (figure S7). These peaks correspond to the two different tree topologies regarding Allotheria. One peak, where the Late Triassic *Haramiyavia* and *Thomasia* formed a clade with other allotherians

(essentially the parsimony result) had a low prior (or tree model likelihood) but a high likelihood (figure S8–9). The other peak, which had *Haramiyavia* and *Thomasia* closer to the root of the tree, and separated from other allotherians, had a higher prior and lower likelihood (figure S10). Overall, allotherian monophyly remained the preferred hypothesis, found in 73% of the posterior sample, compared with 27% showing polyphyly of Allotheria. *Arboroharamiyavia,* the only euharamiyidan included in the Krause *et al.* [2] dataset, was always recovered with multituberculates. A constrained parsimony search revealed that polyphyly of Allotheria requires four additional steps (a 2.23% increase in tree length) compared to the unconstrained analysis (which recovers allotherian monophyly). However, constrained and unconstrained trees were not significantly different (p=0.68) under the Templeton test [37].

*Age of* Juramaia

Rerunning the analysis on the Huttenlocker *et al.* [3] dataset without a hard upper or lower bound on the age of *Juramaia* had no effect on the recovered relationships of haramiyidans and multituberculates: haramiyidan diphyly (and allotherian triphyly) was still recovered (figure S11). Strikingly, however, this analysis revealed a strong signal in the data supporting a post-Jurassic age for *Juramaia* (figure 3). The mean estimated age for *Juramaia* was 123.5 Ma, almost exactly the same as the age of the Jehol Biota, from where several fossil eutherians are known that are morphologically similar to *Juramaia* [22]. The 95% HPD interval was 106.3 – 137.6 Ma, entirely within the Early Cretaceous. This contrasts with the results from the other Yanliao Biota mammaliaforms. When these were assigned the same Laplace distribution age prior as *Juramaia*, the resulting age estimates were always Jurassic. *Megaconus* resulted in the most inaccurate age estimate (mean 173.6 Ma), but the 95% HPD interval (154.8 – 194.8 Ma) comfortably overlapped the true age of the Yanliao Biota. For all other taxa, mean age estimates were between 156.8 Ma (*Rugosodon*) and 164.1 Ma (*Castorocauda)* and 95% HPD intervals fell between 142.6 Ma (lower bound for *Rugosodon*) and 182.4 Ma (upper bound for *Maiopatagium*). The *Juramaia* result may be partly driven by low sampling of eutherians during the Early Cretaceous (supplementary text; figure S12): estimating the age of *Rugosodon* after deleting the similarly-aged multituberculate *Kuehneodon* and plagiaulacids resulted in a wide age estimate (95% HPD 114.4–164.5 Ma).

The age of *Juramaia* also has a significant effect on estimated rates of evolution (figure S13a). When *Juramaia* is assigned its correct, Middle-Late Jurassic age, rates of evolution on the branch leading to crown Theria, and the branch leading to Eutheria, are estimated to be the highest across the entire tree and nearly ten times higher than the average for all branches, as previously reported by *Close et al. [39]*. The rate on the branch leading to Eutheria excluding *Juramaia* is however very low, suggesting a 50-fold decrease in evolutionary rates in eutherians across the Jurassic-Cretaceous boundary. However, when the age of *Juramaia* is allowed to vary (resulting in the estimation of an Early Cretaceous age), rates of evolution on these three branches are far more similar, resulting in approximately constant rates during early eutherian evolution (figure S13b).

# Discussion

*Allotherian relationships*

The results of our tip-dated analysis of the Huttenlocker *et al.* dataset suggest that the dental similarities proposed to unite Allotheria are homoplastic, and that they evolved at least three times independently: once in the common ancestor of *Haramiyavia*+*Thomasia* and tritylodontids, once in the common ancestor of euharamiyidans, hahnodontids and gondwanatherians, and once in multituberculates (*contra* [4, 5, 8, 15, 40]). Notably, a recent study found that dental characters in mammals are more prone to homoplasy than characters from the rest of the skeleton [41]. Our results are congruent with recently discovered morphological differences between Triassic haramiyidans and the euharamiyidans. In particular, *Haramiyavia* retains a prominent postdentary trough [13], a plesiomorphic feature indicating that it lacked fully detached ear ossicles, whereas in most euharamiyidans (with the notable exceptions of *Megaconus* and *Vilevolodon* [12, 16, 42]) this trough is either very small or absent [7-10, 16]. In some ways, our results represent a compromise between differing views on whether haramiyidans are crown- or stem-mammals: euharamiyidans fall within or near the crown-clade, whereas *Haramiyavia*+*Thomasia* fall outside. Our analysis places *Haramiyavia* and *Thomasia* in a clade with tritylodontids, a result that may be the result of insufficient sampling of non-mammaliaform cynodont characters and taxa, and which we consider in need of further testing (see detailed discussion in supplementary information).

The recovered phylogenetic relationships of allotherians depend on both the dataset and the method used. Tip-dated methods invariably push the results towards splitting up the allotherians, but the extent of this depends on the data matrix. For the Krause *et al.* and Wang *et al.* datasets, which originally recovered allotherian monophyly (figure 1, topology 1), tip dating leads to increased support for two independent lineages (figure 1, topology 2b), a topology possibly supported by

recently discovered morphological similarities between early multituberculates and euharamiyids [24]. For the dataset from Huttenlocker *et al.*, which originally recovered separate haramiyidans and multituberculates (topology 2a), tip dating decisively supports three independent lineages (topology 3).

The relative influence of stratigraphic and morphological data in tip-dated analyses remains an underexplored issue. Tip dating of the Huttenlocker *et al.* [3] dataset results in strong support for polyphyly of Allotheria, including diphyly of the haramiyidans, a result that requires only two additional steps under parsimony. In contrast, the dataset of Krause *et al.* [2] has stronger morphological support for allotherian monophyly. Analysis of this dataset flips between allotherian polyphyly and monophyly, and allotherian polyphyly requires four additional parsimony steps over monophyly. In the case of the Krause *et al.* [2] dataset, the stronger morphological signal for allotherian monophyly is therefore not fully overruled by the stratigraphic evidence. These results suggest that the stratigraphic data only become influential on tree topology when morphological support for conflicting topologies is weak. The effect of stratigraphic age on haramiyidan relationships is analysed quantitatively in the supplementary information.

*Age of* Juramaia

For some datasets at least, Bayesian tip dating appears to perform relatively well at estimating the ages of tips when treated as unknown [26], although 95% HPDs can be wide [43]. However, in this case, this method failed to accurately identify *Juramaia* as Middle–Late Jurassic in age, confirming that this taxon is characterised by a morphology that is unusually derived given its age. The Jurassic age of *Juramaia* suggests unusually rapid rates of evolution at the base of therians and eutherians, followed by a 50-fold rate decrease and a period of exceptionally slow eutherian morphological evolution during the Early Cretaceous [39].

The *Juramaia* result requires further scrutiny due to low sampling and phylogenetic uncertainty of early therian mammals (supplementary text; figure S12). Our result is largely driven by two taxa, both of which are known from single specimens: *Juramaia* and *Eomaia*. The highly incomplete record of early eutherians [22] makes it difficult to reach robust conclusions regarding the macroevolution of the group, and these may change with future discoveries. *Juramaia* has also been considered to be a stem therian by some authors [44], a phylogenetic position that would be more consistent with its age. Finally, *Sinodelphys* has recently been proposed to be a eutherian rather than a metatherian [22]. If this is the case, it could alter branch length estimates, and influence inferred patterns of early eutherian evolution.

## Data Accessibility

Full data, analysis code, files and results are on figshare (https://doi.org/10.6084/m9.figshare.8040158).

## Acknowledgements

BK thanks Martin Rücklin for generously supporting the completion of this paper. We thank Brian Davis, Guillermo Rougier, Erik Seiffert, Ian Corfe, Mike Lee, David Grossnickle, Lucas Weaver and an anonymous reviewer for their insightful and constructive comments that much improved the paper. TNT is made freely available through the Willi Hennig society.

## References

1. Kielan-Jaworowska Z., Cifelli R.L., Luo Z.-X. 2004 *Mammals from the age of dinosaurs: origins, evolution, and structure*, Columbia University Press.

2. Krause D.W., Hoffmann S., Wible J.R., Kirk E.C., Schultz J.A., von Koenigswald W., Groenke J.R., Rossie J.B., O'Connor P.M., Seiffert E.R. 2014 First cranial remains of a gondwanatherian mammal reveal remarkable mosaicism. *Nature* **515**(7528), 512–517.

3. Huttenlocker A.K., Grossnickle D.M., Kirkland J.I., Schultz J.A., Luo Z.-X. 2018 Late-surviving stem mammal links the lowermost Cretaceous of North America and Gondwana. *Nature* **558**(7708), 108–112.

4. Butler P.M. 2000 Review of the early allotherian mammals. *Acta Palaeontol Pol* **45**(4), 317–342.

5. Butler P.M., Hooker J.J. 2005 New teeth of allotherian mammals from the English Bathonian, including the earliest multituberculates. *Acta Palaeontol Pol* **50**(2), 185–207.

6. Mao F., Meng J. 2019 Tooth microwear and occlusal modes of euharamiyidans from the Jurassic Yanliao Biota reveal mosaic tooth evolution in Mesozoic allotherian mammals. *Palaeontology* **62**(4), 639–660.

7. Zheng X., Bi S., Wang X., Meng J. 2013 A new arboreal haramiyid shows the diversity of crown mammals in the Jurassic period. *Nature* **500**(7461), 199–202.

8. Bi S., Wang Y., Guan J., Sheng X., Meng J. 2014 Three new Jurassic euharamiyidan species reinforce early divergence of mammals. *Nature* **514**(7524), 579–584.

9. Meng J., Bi S., Zheng X., Wang X. 2018 Ear ossicle morphology of the Jurassic euharamiyidan *Arboroharamiya* and evolution of mammalian middle ear. *J Morphol* **279**(4), 441–457.

10. Chang S.-C., Gao K.-Q., Zhou C.-F., Jourdan F. 2017 New chronostratigraphic constraints on the Yixian Formation with implications for the Jehol Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology* **487**, 399–406.

11. Zhou C.-F., Wu S., Martin T., Luo Z.-X. 2013 A Jurassic mammaliaform and the earliest mammalian evolutionary adaptations. *Nature* **500**(7461), 163–167.

12. Luo Z.-X., Meng Q.-J., Grossnickle D.M., Liu D., Neander A.I., Zhang Y.-G., Ji Q. 2017 New evidence for mammaliaform ear evolution and feeding adaptation in a Jurassic ecosystem. *Nature* **548**(7667), 326–329.

13. Luo Z.-X., Gatesy S.M., Jenkins F.A., Amaral W.W., Shubin N.H. 2015 Mandibular and dental characteristics of Late Triassic mammaliaform *Haramiyavia* and their ramifications for basal mammal evolution. *Proceedings of the National Academy of Sciences* **112**(51), E7101–E7109.

14. Krause D.W., Hoffmann S., Hu Y., Wible J.R., Rougier G.W., Kirk E.C., Groenke J.R., Rogers R.R., Rossie J.B., Schultz J.A. 2020 Skeleton of a Cretaceous mammal from Madagascar reflects long-term insularity. *Nature*, https://doi.org/10.1038/s41586-41020-42234-41588.

15. Wang H., Meng J., Wang Y. 2019 Cretaceous fossil reveals a new pattern in mammalian middle ear evolution. *Nature* **576**(7785), 102–105.

16. Meng J., Mao F., Han G., Zheng X.T., Wang X.L., Wang Y. 2020 A comparative study on auditory and hyoid bones of Jurassic euharamiyidans and contrasting evidence for mammalian middle ear evolution. *J Anat* **236**(1), 50–71.

17. Rougier G.W., Martinelli A.G., Forasiepi A.M., Novacek M.J. 2007 New Jurassic mammals from Patagonia, Argentina: a reappraisal of australosphenidan morphology and interrelationships. *Am Mus Novit* **3566**, 1–54.

297 18. Luo Z.-X., Yuan C.-X., Meng Q.-J., Ji Q. 2011 A Jurassic eutherian mammal and divergence of
298 marsupials and placentals. *Nature* **476**(7361), 442–445.
299 19. Xu X., Zhou Z., Sullivan C., Wang Y., Ren D. 2016 An Updated Review of the Middle-Late
300 Jurassic Yanliao Biota: Chronology, Taphonomy, Paleontology and Paleoecology. *Acta Geologica*
301 *Sinica (English Edition)* **90**(6), 2229–2243.
302 20. Meng J. 2014 Mesozoic mammals of China: implications for phylogeny and early evolution of
303 mammals. *National Science Review* **1**(4), 521–542.
304 21. Sullivan C., Wang Y., Hone D.W., Wang Y., Xu X., Zhang F. 2014 The vertebrates of the
305 Jurassic Daohugou Biota of northeastern China. *J Vertebr Paleontol* **34**(2), 243–280.
306 22. Bi S., Zheng X., Wang X., Cignetti N.E., Yang S., Wible J.R. 2018 An Early Cretaceous eutherian
307 and the placental–marsupial dichotomy. *Nature* **558**, 390–395.
308 23. Ronquist F., Klopfstein S., Vilhelmsen L., Schulmeister S., Murray D.L., Rasnitsyn A.P. 2012 A
309 total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera.
310 *Syst Biol* **61**(6), 973–999.
311 24. Averianov A.O., Martin T., Lopatin A.V., Schultz J.A., Schellhorn R., Krasnolutskii S., Skutschas
312 P., Ivantsov S. 2020 Multituberculate mammals from the Middle Jurassic of Western Siberia, Russia,
313 and the origin of Multituberculata. *Papers in Palaeontology*,
314 https://doi.org/10.5061/dryad.rfj5066q5776.
315 25. Lee M.S.Y., Yates A.M. 2018 Tip-dating and homoplasy: reconciling the shallow molecular
316 divergences of modern gharials with their long fossil record. *Proc R Soc B* **285**(1881), 20181071.
317 26. Drummond A.J., Stadler T. 2016 Bayesian phylogenetic estimation of fossil ages. *Philos Trans*
318 *R Soc B* **371**(1699), 20150129.
319 27. Sallam H.M., Seiffert E.R. 2016 New phiomorph rodents from the latest Eocene of Egypt, and
320 the impact of Bayesian "clock"-based phylogenetic methods on estimates of basal hystricognath
321 relationships and biochronology. *PeerJ* **4**, e1717.

28. Bouckaert R., Vaughan T.G., Barido-Sottani J., Duchêne S., Fourment M., Gavryushkina A., Heled J., Jones G., Kühnert D., De Maio N., et al. 2019 BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Comput Biol* **15**(4), e1006650.

29. Lewis P.O. 2001 A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst Biol* **50**(6), 913–925.

30. Drummond A.J., Ho S.Y., Phillips M.J., Rambaut A. 2006 Relaxed phylogenetics and dating with confidence. *PLoS Biol* **4**(5), e88.

31. Gavryushkina A., Welch D., Stadler T., Drummond A.J. 2014 Bayesian inference of sampled ancestor trees for epidemiology and fossil calibration. *PLoS Comput Biol* **10**(12), e1003919.

32. Rambaut A., Drummond A.J., Xie D., Baele G., Suchard M.A. 2018 Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst Biol* **67**(5), 901–904.

33. Warren D.L., Geneva A.J., Lanfear R. 2017 RWTY (R We There Yet): An R package for examining convergence of Bayesian phylogenetic analyses. *Mol Biol Evol* **34**(4), 1016-1020.

34. Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. 2012 MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol* **61**(3), 539–542.

35. Goloboff P.A., Farris J.S., Nixon K.C. 2008 TNT, a free program for phylogenetic analysis. *Cladistics* **24**(5), 774–786.

36. Jombart T., Aanensen D.M., Baguelin M., Birrell P., Cauchemez S., Camacho A., Colijn C., Collins C., Cori A., Didelot X. 2014 OutbreakTools: A new platform for disease outbreak analysis using the R software. *Epidemics* **7**, 28–34.

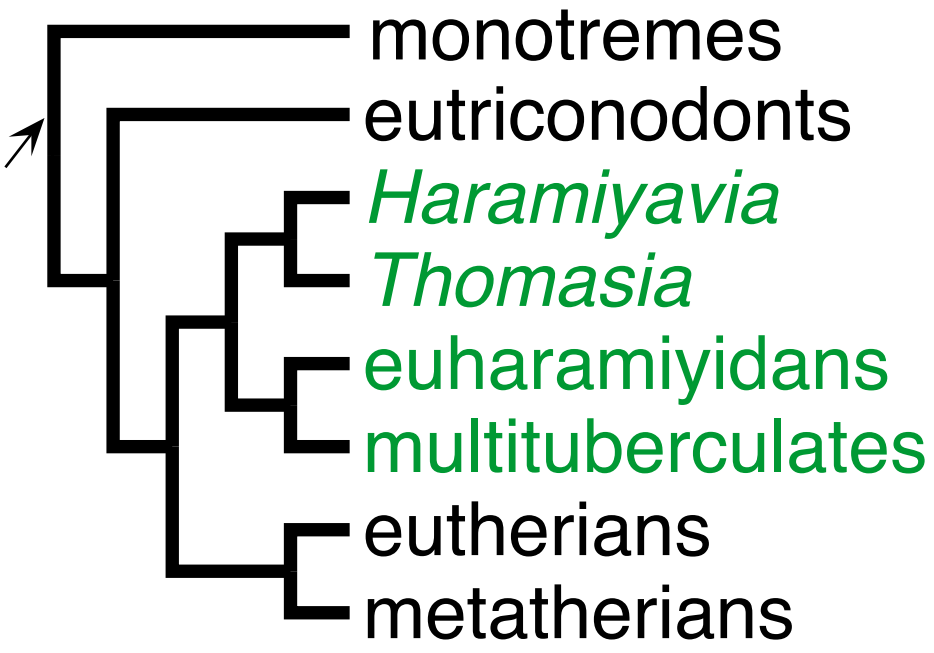
37. Templeton A.R. 1983 Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* **37**(2), 221–244.

38. Jenkins F.A., Gatesy S.M., Shubin N.H., Amaral W.W. 1997 Haramiyids and Triassic mammalian evolution. *Nature* **385**(6618), 715–718.

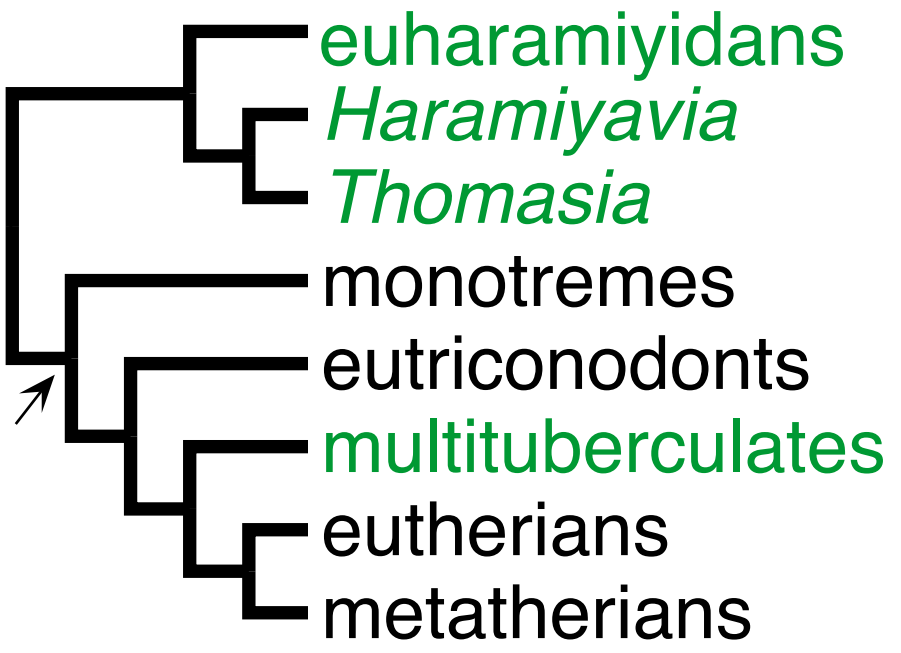
347 39. Close R.A., Friedman M., Lloyd G.T., Benson R.B. 2015 Evidence for a mid-Jurassic adaptive
348 radiation in mammals. *Curr Biol* **25**(16), 2137–2142.
349 40. Han G., Mao F., Bi S., Wang Y., Meng J. 2017 A Jurassic gliding euharamiyidan mammal with
350 an ear of five auditory bones. *Nature* **551**(7681), 451-456.
351 41. Sansom R.S., Wills M.A., Williams T. 2017 Dental data perform relatively poorly in
352 reconstructing mammal phylogenies: morphological partitions evaluated with molecular
353 benchmarks. *Syst Biol* **66**(5), 813-822.
354 42. Meng J., Bi S., Wang Y., Zheng X., Wang X. 2014 Dental and mandibular morphologies of
355 Arboroharamiya (Haramiyida, Mammalia): a comparison with other haramiyidans and *Megaconus*
356 and implications for mammalian evolution. *PloS one* **9**(12), e113847.
357 43. Dembo M., Radovčić D., Garvin H.M., Laird M.F., Schroeder L., Scott J.E., Brophy J.,
358 Ackermann R.R., Musiba C.M., de Ruiter D.J. 2016 The evolutionary relationships and age of *Homo*
359 *naledi*: An assessment using dated Bayesian phylogenetic methods. *J Hum Evol* **97**, 17–26.
360 44. Sweetman S., Smith G., Martill D. 2017 Highly derived eutherian mammals from the earliest
361 Cretaceous of southern Britain. *Acta Palaeontol Pol* **62**, 657–665.

362

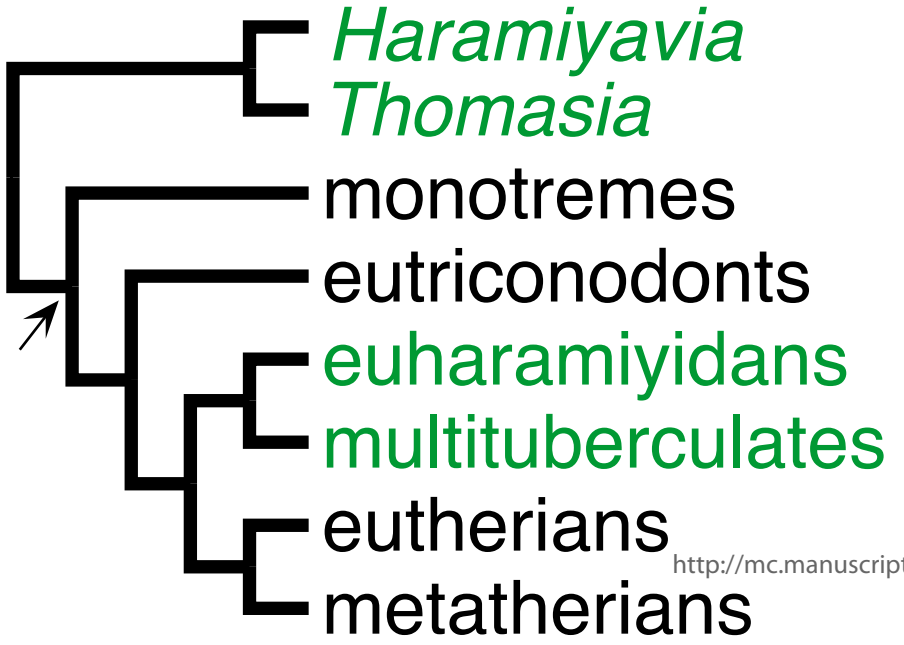
1 allotherians monophyletic



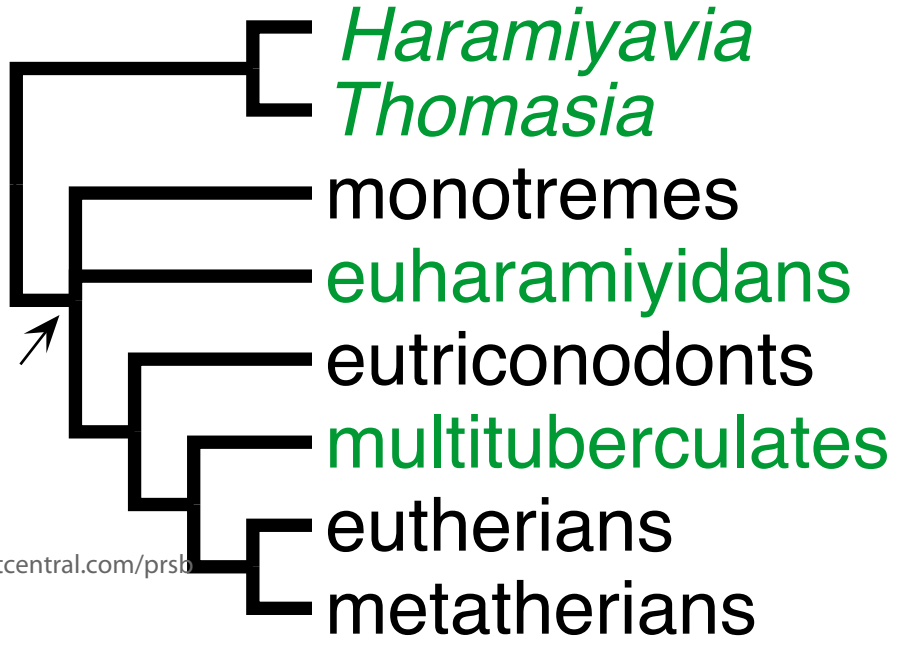

2a haramiyidans monophyletic

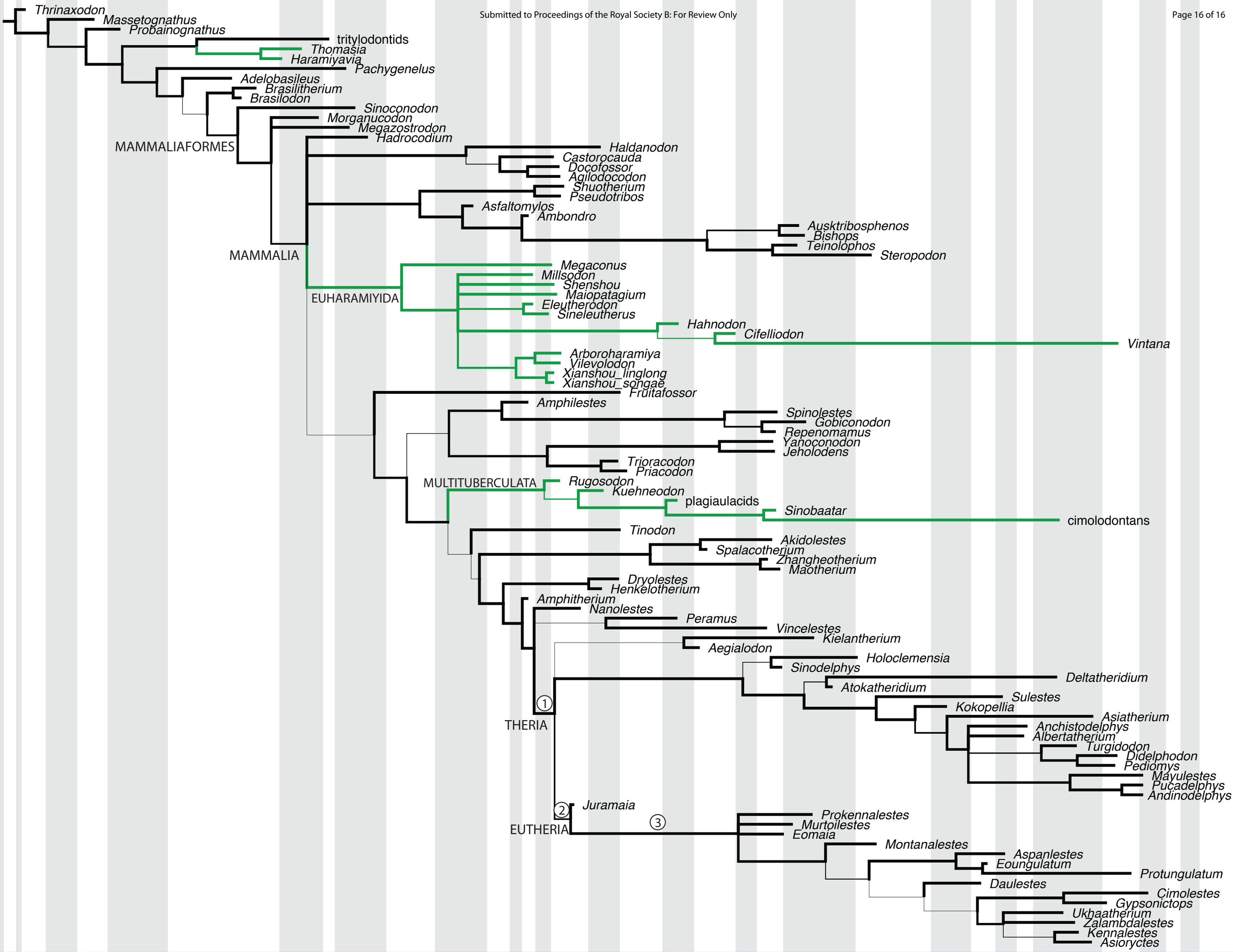



2b euharamiyidans and multituberculates monophyletic




3 allotherians polyphyletic




Thrinaxodon
Massetognathus
Probainognathus
tritylodontids
Thomasia
Haramiyavia
Pachygenelus
Adelobasileus
Brasilitherium
Brasilodon
Sinoconodon
Morganucodon
Megazostrodon
Hadrocodium
MAMMALIAFORMES
Haldanodon
Castorocauda
Docofossor
Agilodocodon
Shuotherium
Pseudotribos
Asfaltomylos
Ambondro
Ausktribosphenos
Bishops
Teinolophos
Steropodon
MAMMALIA
Megaconus
Millsodon
Shenshou
Maiopatagium
Eleutherodon
Sineleutherus
EUHARAMIYIDA
Hahnodon
Cifelliodon
Vintana
Arboroharamiya
Vilevolodon
Xianshou_linglong
Xianshou_songae
Fruitafossor
Amphilestes
Spinolestes
Gobiconodon
Repenomamus
Yanoconodon
Jeholodens
Trioracodon
Priacodon
MULTITUBERCULATA
Rugosodon
Kuehneodon
plagiaulacids
Sinobaatar
cimolodontans
Tinodon
Akidolestes
Spalacotherium
Zhangheotherium
Maotherium
Dryolestes
Henkelotherium
Amphitherium
Nanolestes
Peramus
Vincelestes
Kielantherium
Aegialodon
Holoclemensia
Sinodelphys
Deltatheridium
Atokatheridium
Sulestes
Kokopellia
Asiatherium
Anchistodelphys
Albertatherium
Turgidodon
Didelphodon
Pediomys
Mayulestes
Pucadelphys
Andinodelphys
1
THERIA
2
Juramaia
EUTHERIA
3
Prokennalestes
Murtoilestes
Eomaia
Montanalestes
Aspanlestes
Eoungulatum
Protungulatum
Daulestes
Cimolestes
Gypsonictops
Ukhaatherium
Zalambdalestes
Kennalestes
Asioryctes
Wuchiapingian
Changhsingian
Induan
Olenekian
Anisian
Ladinian
Carnian
Norian
Rhaetian
Hettangian
Sinemurian
Pliensbachian
Toarcian
Aalenian
Bajocian
Bathonian
Callovian
Oxfordian
Kimmeridgian
Tithonian
Berriasian
Valanginian
Hauterivian
Barremian
Aptian
Albian
Cenomanian
Turonian
Coniacian
Santonian
Campanian
Maastrichtian
Danian
Selandian
Thanetian
Ypresian
pingian
Lower
Middle
Upper
Lower
Middle
Upper
Lower
Upper
Paleocene
Eocen
mian
Triassic
Jurassic
Cretaceous
Paleogene
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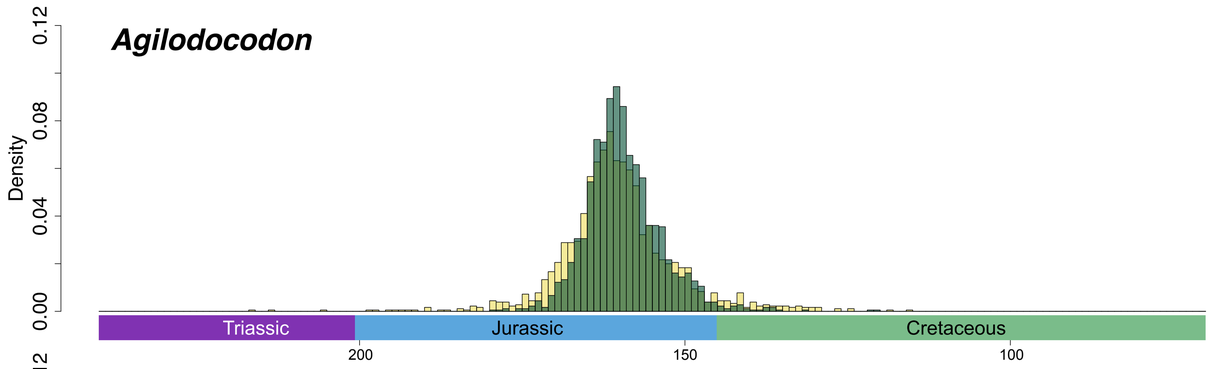
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Triassic
Jurassic
Cretaceous
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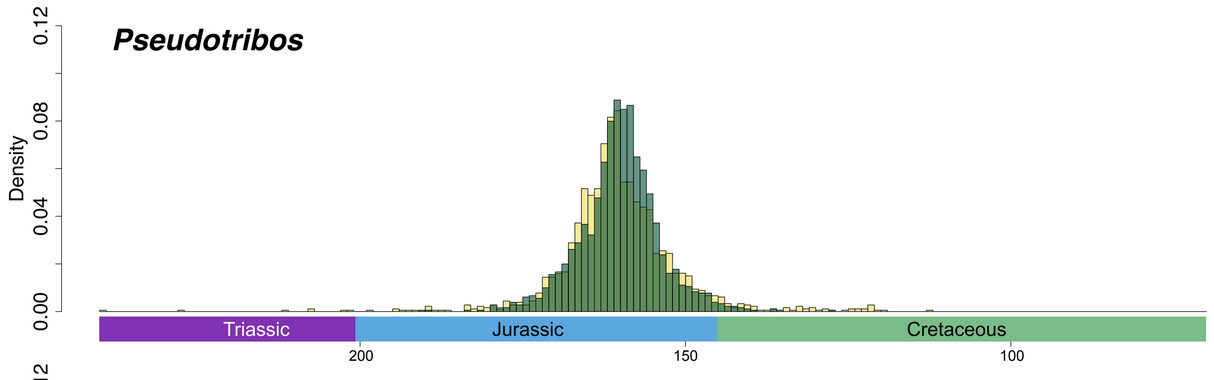
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Density
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Triassic
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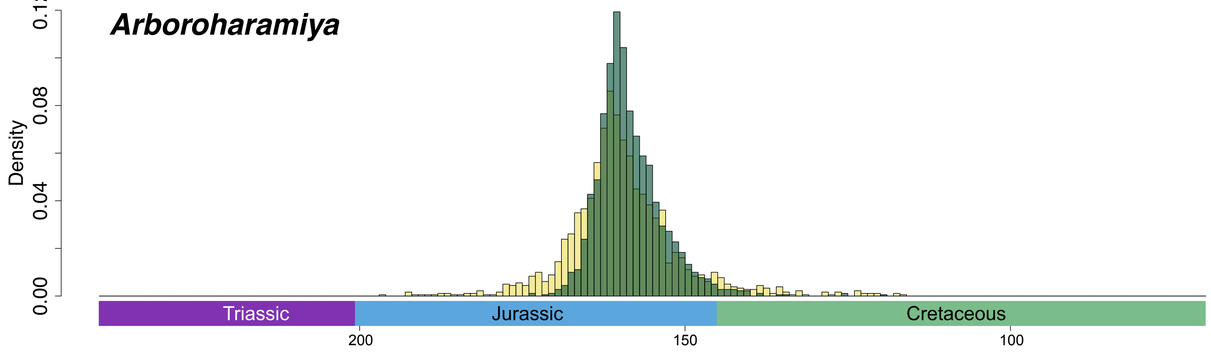
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Triassic
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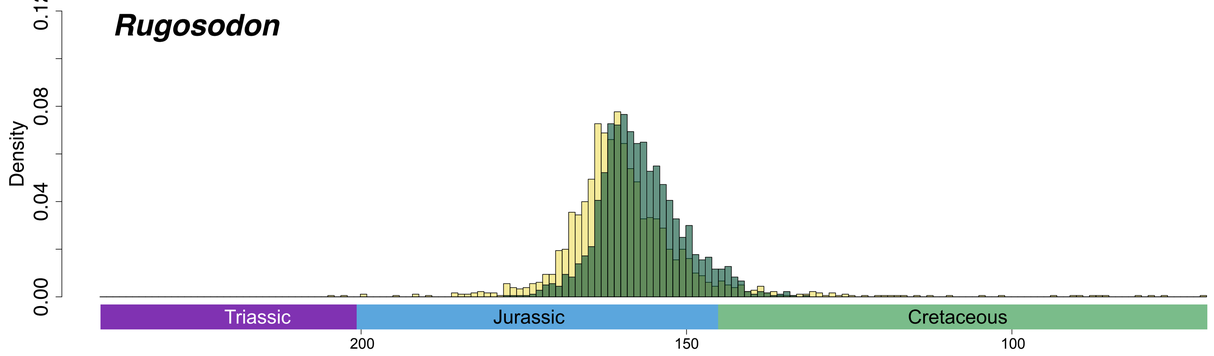
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Density
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Triassic
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Cretaceous
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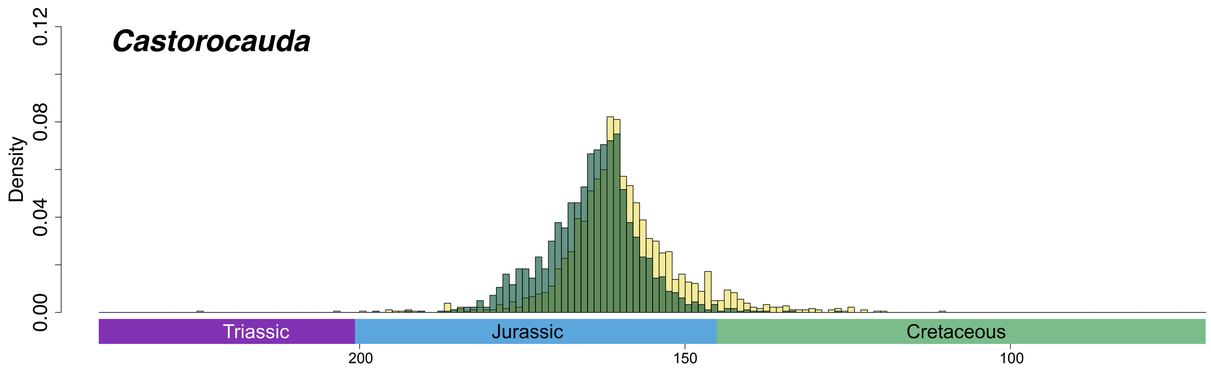
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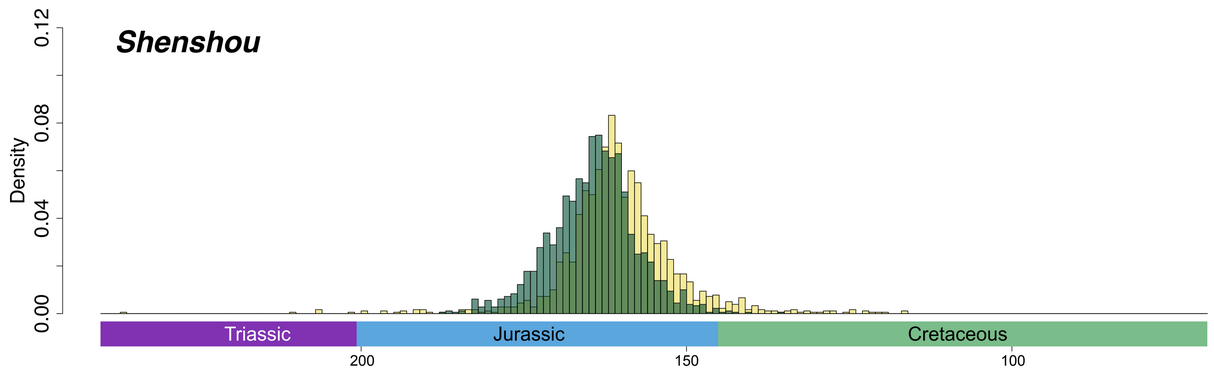
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Density
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Triassic
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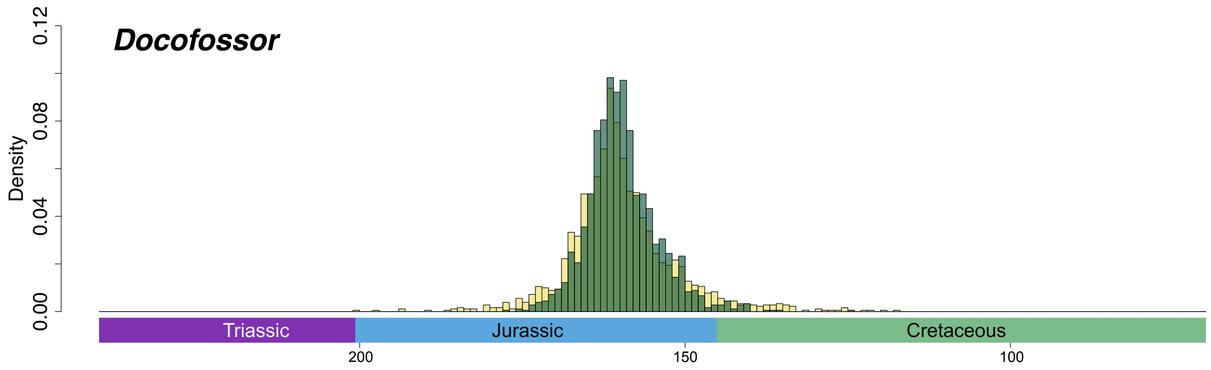
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Density
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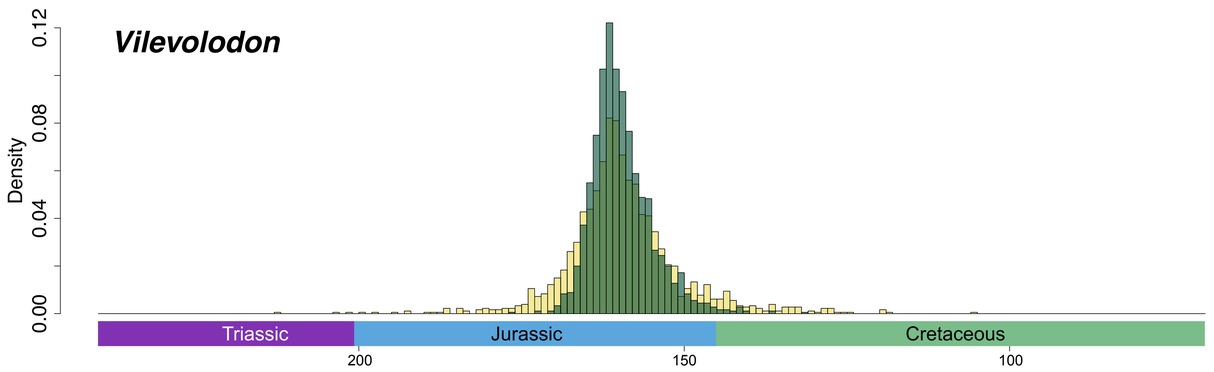
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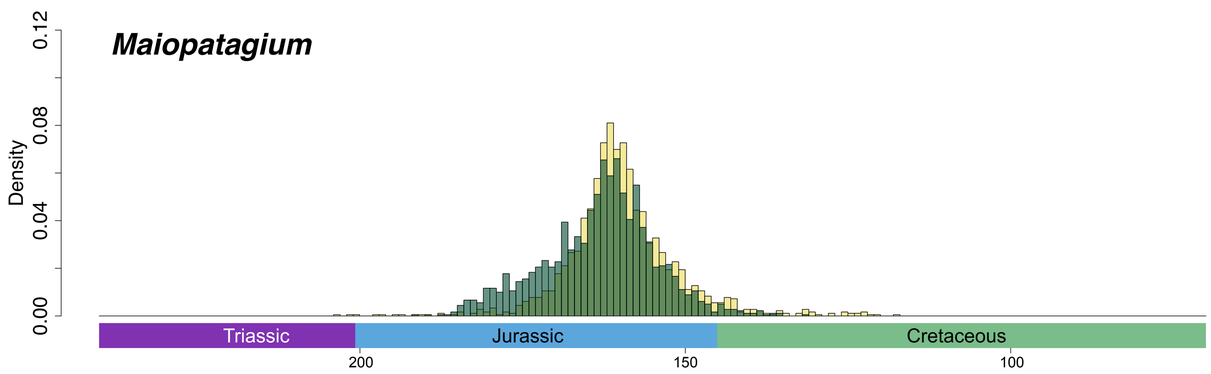
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Density
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Triassic
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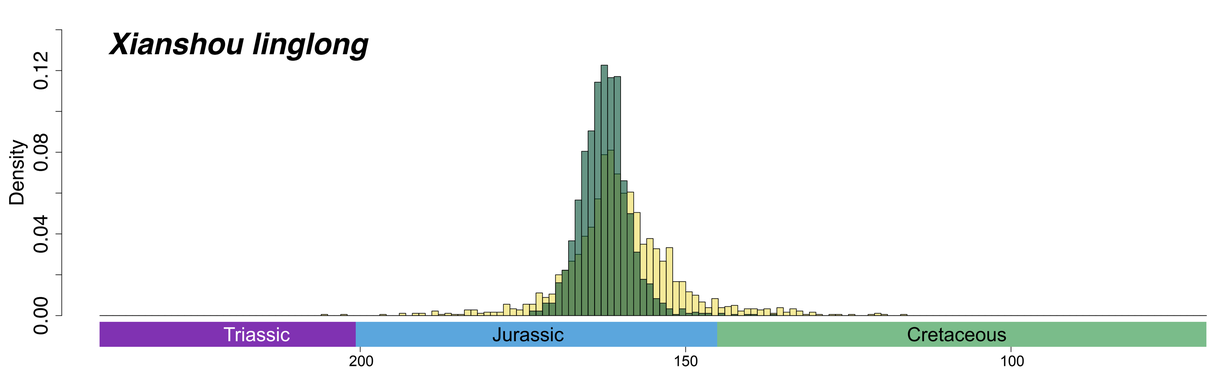
Xianshou linglong
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Triassic
Jurassic
Cretaceous
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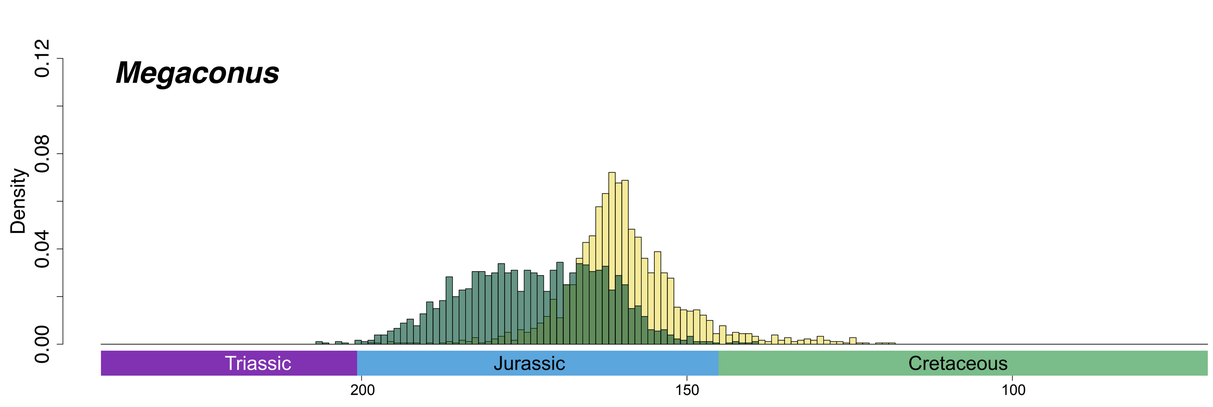
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Density
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Jurassic
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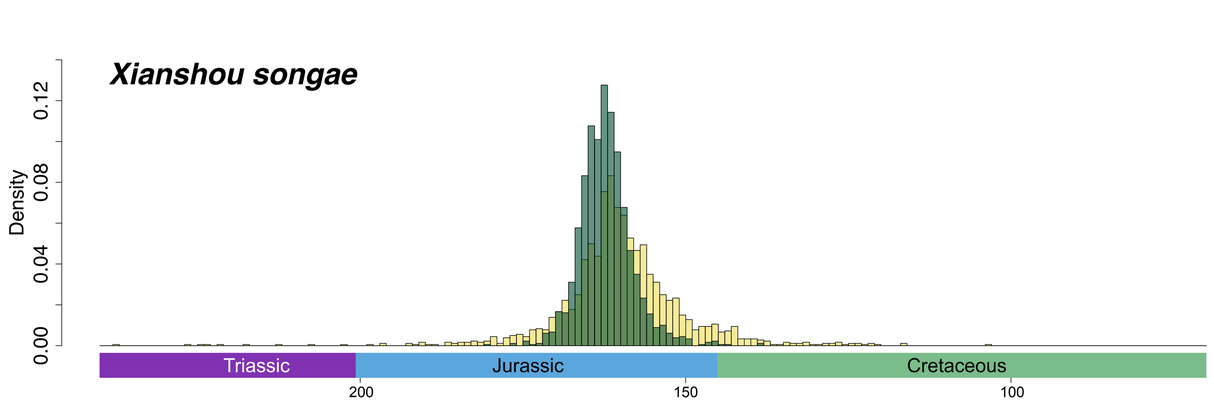
Xianshou songae
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Triassic
Jurassic
Cretaceous
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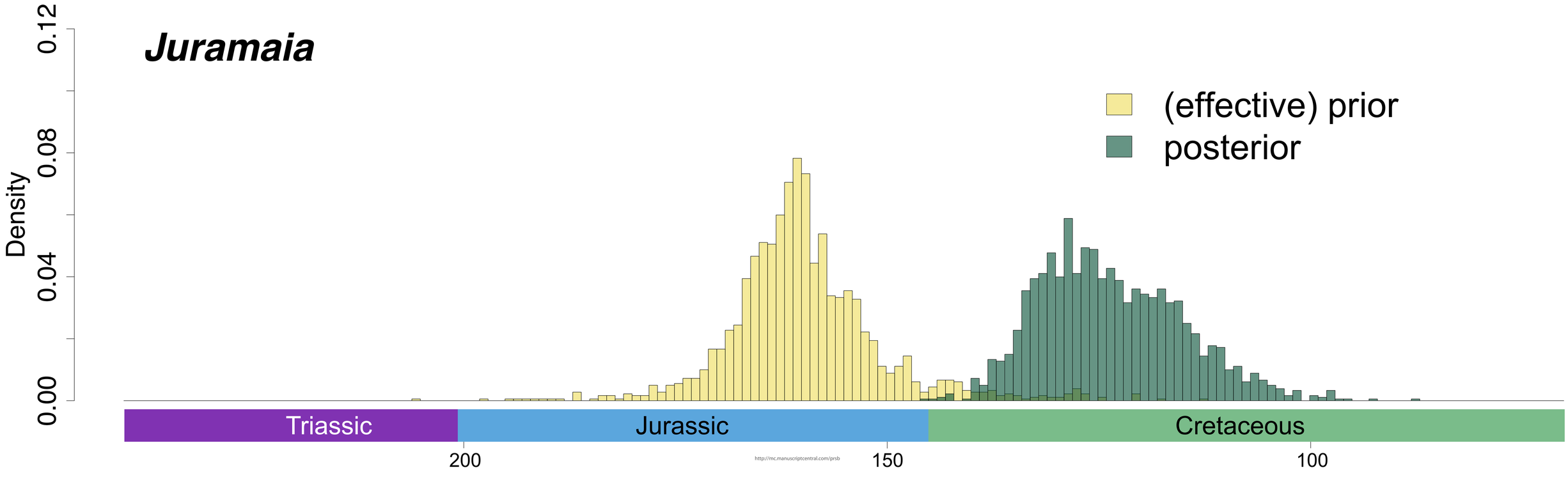
Juramaia
(effective) prior
posterior
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Triassic
Jurassic
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